DOI: 10.1007/s11676-007-0009-9

Review on the decomposition and influence factors of coarse woody debris in forest ecosystem

ZHOU Li[1, 2], DAI Li-min[1], GU Hui-yan[1, 3], ZHONG Lei[1, 2]

[1] *Institute of Applied Ecology, Chinese Academy of Science, Shenyang 110016, P. R. China*
[2] *Graduate School of Chinese Academy of Science, Beijing 100039, P. R. China*
[3] *Northeast Forestry University, Harbin 150040, P. R. China*

Abstract: Coarse woody debris (CWD) is an important and particular component of forest ecosystems and is extremely important to forest health. This review describes the decomposition process, decomposition model and influence factors. CWD decomposition is a complex and continuous process and characterizes many biological and physical processes, including biological respiration, leaching, and fragmentation. All these processes have closed relationships between each other and work synergistically. During decomposition, there are many controlling factors mainly including site conditions (temperature, humidity, and O_2/CO_2 concentration), woody substrate quality (diameter, species and compound) and organism in CWD. The decomposition rate is generally expresses through a constant k which indicate the percent mass, volume or density loss over time, and can be determined by long-term monitoring, chronosequence approach and the radio between input and the total mass. Now using mathematical models to simulate decomposition patterns and estimate the decomposition rate is widely applied, especially the exponential model. We brought forward that managing and utilizing for the CWD in forest was a primary objective on all forest lands. And it is should be intensified to integrate many related research subjects and to carry a comprehensive, long-term and multi-scale research which mainly focus on seven sections.

Keywords: Coarse woody debris, Decomposition, Forest ecosystem; Influence factors

Introduction

Coarse woody debris (CWD) is the residue of living trees in the forest ecosystem including whole fallen trees, fallen branches, and pieces of fragmented wood, stumps and standing dead trees (snags). Historically it was poorly understood because people regarded it as the main factors to cause the tree diseases, insect pests and forest fire. However, along with the embedded research in forest ecosystem especially in nutrient cycles and global warming, people realized that CWD is a particular component of forest ecosystems and extremely important to forest health. CWD serves a variety of essential functions in the forest ecosystem. It provides seed germination sites (Harmon *et al*. 1986 & 1989; Graham and Cromack 1982; Gray and Spies 1997; Xu 1998), serves as reservoirs during droughts (Deng *et al*. 2002; Harmon and Sexton 1995; Zhao *et al*. 2002), and provides habitats for many forest animals (Rabe *et al*. 1998; Timothy and Mark 2004; Torgersen and Bull 1995) and microbes (Amaranthus *et al*. 1994). Moreover, CWD also plays an integral role in the material flow, energy flow and nutrient cycling in forest ecosystems. CWD can release the plentiful carbon, nitrogen, phosphorus and other nutrients gradually and tardily by its decomposition, just like the controlled release chemical fertilizer (Turner *et al*. 1995; Janisch and Harmon 2001; Holub *et al*. 2001; Mackensen 2003). So CWD can enhance the upper forest soil fertility and productivity (Marra and Edmonds 1994; Mcminn and Crossley 1993), promote the forest restoration and natural regeneration after harvesting, protect the ecosystem from disturbance-related nutrient losses, and maintain the biodiversity, stability and balance of forest ecosystem (Zimmerman *et al*. 1995; Wei *et al*. 1997; Arthur and Fahey 1990; Harmon *et al*. 1990). At present, most of the studies focused on ecological role, stocks, distribution and dynamics (Harmon *et al*. 1987; Niklas *et al*. 2005; Friaman and Walheim 2000; Woldendorp *et al*. 2004) except a few paid attention to CWD decomposition and nutrient release systematically (Girisha *et al*. 2004; Raija *et al*. 2004). In China, research on CWD mainly concerned the concept (Yan *et al*. 2005), function (Wu *et al*. 2005; Liu *et al*. 2004; Hou and Pan 2001) and stocks of different forest type, such as Korean pine mixed forest (Chen and Xu 1992; Li 1992b; Zhao 1995; Dai *et al*. 2002), Fargesii (Li *et al*. 1998), Castanopsis eyrei (Li *et al*. 1996), evergreen broadleaved forest (Liu *et al*. 1995; Tang *et al*. 2003), and dark-conifer forest (Yang *et al*. 2002a & 2002b). It can not be neglected that the decomposition will determine the longevity and turnover of carbon stored in CWD, which in turn determines the amount of CO_2 released from forest ecosystem. Knowledge of the decomposition will provide information for the calculation CO_2 emission from land-use change and forest management practices, and will also provide information on the nutrients released into the soil pool, so the CWD decomposition is also very important for several aspects of forest management (Mackensen

Foundation project: This research was supported by National Natural Science Foundation of China (No.30470302&70373044), Overseas Scholar Funding from Chinese Academy of Science (C13HU&C13HK).

Received: 2006-06-20; Accepted: 2006-09-15

Electronic supplementary material is available in the online version of this article at http://dxdoi.org/10.1007/s11676-007-0009-9

Biography: ZHOU Li (1977-), female, assistant professor, Ph.D. candidate in Institute of Applied Ecology, Chinese Academy of Science, Shenyang 110016, P. R. China. Email: iaezhouli@126.com

Responsible editor: Song Funan

2003). In this paper, we provide a comprehensive review to document the processes and rates of CWD decomposition and to identify the influence factors during the process of decomposition. Hoping it can fill up some blanks of the research and establish the corresponding groundwork for further research on CWD decomposition.

Decomposition process

Decomposition is the process whereby the complex organic structure of biological material such as wood is reduced to its mineral form. Also the decomposition or depletion of CWD involves many different biological and physical processes (Harmon *et al*. 1986; Golladay and Webster 1988). It includes the transformation of both carbon and all the macro-and micro-nutrients (Swift 1977). Apart from the biochemical aspects of decomposition (biological respiration and transformation), this term is often used in a wider context that includes the physical-chemical deterioration of organic matter due to photodegradation, leaching and fragmentation.

Biological respiration

The large biomass of CWD represents the largest pool of organic carbon in many forests (Fahey 1983; Boone *et al*. 1988). During the decay process, the invasion and respiration of different species of microbes and invertebrates make an initial mass loss and break down of approximately 50% organic carbon leading to a release of carbon as CO_2 gas (Spies *et al*. 1988). Global carbon cycle is defined as the cyclical movement of carbon within the biosphere. Carbon is primarily removed by plants during photosynthesis and then dissolved in water and returned to the air mainly via biological respiration. Swift (1973) indicated that most of microbes and invertebrates can utilize the organic matter of CWD for their own metabolism, especially bacteria and fungi, and the quantity of metabolized organic matter was comparable to the extent of respiration losses. For example, when about 39 percent biomass of CWD was losing, maybe about 35 percent was converting into fungal biomass (Swift 1973).

How much of carbon released and organic matter metabolized depends on respiration rate which is related to the quantity of decomposer and their activity (Li 1992a). Also lots of research results proved that biologic respiration had the seasonal change; generally speaking, decomposer had strong action and hearty metabolism in summer, so there was high respiration rate in that time (Li 1992a). Moreover, the respiration rate has close relationship with the decay class and tree species. Respiration intensity is strengthened along with the decomposition (Ausum 1977; Yoneda 1975).

Leaching

Leaching, which is caused by the physical forces of water, temperature and gravity, can transport nutrients and soluble materials from CWD into soil, break down wood structure and reduce CWD biomass (McMinn and Crossley 1993). Leaching is also considered an important process in CWD decomposition (Singh and Gutpka 1977; Swift *et al*. 1979), although there are very few researches on this topic (Mattson *et al*. 1984 & 1987). In the initial stages of decomposition, there are little soluble materials but more polymers in CWD, so the importance of leaching is not very obvious. However, in the advanced stages of decomposition, the polymers are transformed into soluble materials as a result of degradation of microbe; the more soluble materials strengthen the function of leaching (Harmon *et al*. 1986).

Weathering is also the chemical and physical disintegration of wood by atmospheric elements (Jemison 1937). Because CWD always exposure under the atmosphere, rain, snow, sunlight, dust, humidity, etc.. All these factors can affect the surface layer synthetically leading to become coarseness and looseness due to suffering from expand, shrink, and ultraviolet alternately, then some wood destroying agents such as fungi and termites can easily colonize and decompose the CWD.

Fragmentation

CWD fragmentation refers to a reduction of volume via physical and chemical forces during the decay process. It has two kinds of forms commonly, one is physical causes, the other is biological causes, and we can distinguish them easily (Harmon *et al*, 1986). The former includes breakage during or after falling to the ground or impact from new CWD arrivals, freezing/thawing and shrinkage/swelling cycles forming cracks, wind, snow, rain, flowing water, and use of machinery in managed ecosystem are also important agents of CWD fragmentation. All these causes usually affect on the exterior of CWD. Comparing with physical causes, the biological causes can accelerate the fragmentation by decay organisms because it affects on the interior directly. The main decay organisms are invertebrates and other wood-boring insects, such as bark and ambrosia beetles. Invertebrates chaw the woodiness and dig tunnel, wood-boring insects bore the trunk, and these actions facilitate faster colonization of wood by microbes and thus accelerate the decomposition (Ausmus 1977; Leach 1934). Furthermore, wood habiting invertebrates are the important food sources of some vertebrates such as birds, and their feeding on invertebrates must accelerate the fragmentation. Also the plants that grow on the fallen trees can break up the CWD during the course of their roots' growth and extension.

Fragmentation, collapse and settling are prominent in the snag decomposition process. It can be said that the fragmentation and the decomposition are processed synchronously. After being died, nutrimental matters of snags begin to loss and leaching, that is decomposition. On the other hand, the branches fall to pieces, the trunk also begin to fall off. So the snag becomes short by and by until becomes a residual stake even a ridge surface (Hou and Pan 2001).

Decomposition rate and model

Decomposition rate

The decomposition rate is generally expresses through a constant k which indicates the percent mass, volume or density loss over time (Harmon *et al*. 1986; Swift *et al*. 1979; Mackensen and Bauhus 2003). The higher the k value, the faster CWD decomposes. It is extremely difficult to measure given the extreme longevity (Franklin *et al*. 1987).

The most reliable method to determine the decomposition rate is through long-term monitoring about the changes of volume, wood density or mass to calculate and assess the constant k. But few studies adopted this method because of the long time and vast cost (Chen and Xu 1991). It is therefore more common to establish a chronosequence by take samples from a range of known ages or different decay classes (Lambert *et al*. 1980; Fos-

ter and Lang 1982; Graham and Cromack 1982; Busse 1994; Mark *et al*. 2000; Tyrrell and Crow 1994). The reliability of this method largely depends on the ability to accurately identify the age of CWD and site with comparable conditions (Harmon *et al*. 1986). However, chronosequence studies provide indirect evidence about decomposition rates (i.e., comparison among different logs) and may be subject to confounding effects related to measurement and site. Besides the above two methods, the decomposition rate can also be estimated from the radio between input and the total mass of CWD (Christensen 1977; Sollins 1982; Delaney *et al*. 1998). However, this method has a rigorous precondition that the stand must be stable namely the input of CWD is neither more nor less than the decomposition of CWD. Though this kind of steady state is very difficult to be proved in most of forests for the variance of CWD is often periodical through many nature or human disturbance (Daniel and Dennis 2000; Wei *et al*. 1997).

Decomposition model

Using mathematical models to simulate decomposition patterns and estimate the decomposition rate has been widely applied to quantify the decomposition of CWD (Harmon *et al*. 1986). Several potential models include single-exponential model, double-exponential model, multiple-exponential model (Olson 1963), lag-time model (Harmon *et al*. 1986; Chen and Xu 1991), and linear model (Wieder and Lang 1982; Lambert *et al*. 1980; Graham and Cromack 1982), respectively. Except the last one, the others assume that all constituents of dead biomass are equally decomposable and the constituents of dead woody biomass are equally distributed (Carpenter 1981).

The single-exponential model is the most common multiple linear regression model form used to determine decomposition constants (Olson 1963; Graham and Cromack 1982; Barber and van Lear 1984; Mattson *et al*. 1987; Edmonds and Eglitis 1989; Harmon and Chen 1991; Stone *et al*. 1998; Laiho and Prescott 1999; Chen *et al*. 2001; Janisch and Harmon 2001). Assuming that the proportion of lost remains constant throughout the decomposition process or the decomposition rate is proportional to the amount of matter remaining, the decomposition rate can be derived from the equation bellows: $Yt = Y0e\text{-}kt$, where Yt =amount left at time t, Y0=initial quantity of material, k=decomposition constant.

Minderman (1968) put forward the double and multiple-exponential model against single-exponential model because he found that CWD is not homogeneous but heterogeneous with components decomposing at different rates over time. For example, the heartwood was more decay resistant than sapwood and bark, then the actual results must be different significantly (Mackensen and Bauhus 2003).

The lag-time model takes the lag times required for fungi, bacteria and other macro invertebrates finally succeed in colonizing CWD into account. The lag times for snag fall after death may be as long as 20 years and for log mineralization may exceed 25 years (Harmon *et al*. 1986). However, there are few researches on the factors influencing lag time or their ecological significance (Mackensen and Bauhus 2003)

Influence factors

The main decomposition process of CWD depends on the wood inhabiting organisms' biochemical interaction with wood components which microorganisms and invertebrates are involved (Rayner & Boddy 1988). The close association between insects and decay fungi strongly influences the decomposition rate (Gardiner 1957; Zhong and Schowalter 1989). And these organisms' activities are influenced by the controlling factors such as temperature, humidity, concentration of CO_2 and O_2, and woody substrate quality including species, size, component and position (Harmon 1986). These factors are complex, interactional and interdependent. Studies had proved that single factors can only emphasized to laboratory tests (Boddy 1983) and there is no agreement on which factor may be the key driving factor of decomposition (Swift *et al*. 1979; Bunnell *et al*. 1977; Mikola 1960; Brown *et al*. 1996).

Temperature

Temperature can strongly influence the biological subsistence, and at the same time the temperature is also influenced by many factors such as surrounding temperature, relative humidity, CWD size, bark, position, and so on (Rayner & Boddy 1988). Optimal temperature can shorten the organism's lifecycle, then to accelerate the decomposition (Graham 1925). Many fungi species are mesophilous, the optimal scope for their growth in the wood is between 25–30°C, their respiration will increase by 2-3 for every 10°C increase but they can't survive above 40°C (Kaarik 1974; Hammon 1986; Deverall 1965). Savely (1939) found that the insects could suffer from more high temperature, their upper limits could reach 52°C, but this upper limit would decrease to 41–44°C with the increase of relative humidity. Studies also found that the temperatures on the surface or top of CWD which exposed to sunlight may greatly higher (Graham 1925). Furthermore, the tree species or forest type can also influence the surrounding temperature, then to influence the inner temperature. For example, the annual temperature in Korean-dark coniferous forest is higher than that in Ermanii-dark coniferous forest in Changbai Mountain, especially in July or August. So the subsistence and activity of microbes and invertebrates are stronger in the Korean-dark coniferous forest and the CWD decomposition rate in this kind of forest is comparative higher than those of another forest (Yang *et al*. 2002a).

Humidity

Both high humidity and low humidity in particular can restrict the activity of wood habiting organisms. Fungi, other decomposing microorganisms and insects can't live if the humidity is below 30%. Their activities are improved with the increase of humidity, whereas also limited by a very high humidity (Griffin 1977). Some bacteria and fungi such as the soft rots fungi can survive in the high humidity of 240%. But only 30%–160% is the most optimal humidity for the growth of Basidiomycetes (Kaarik 1974). Humidity and its daily and seasonal fluctuations also depend on the size, position, and microclimate and decay class. Humidity increases with the process of decomposition because it is negatively correlates with wood density.

O_2 and CO_2 concentration

O_2 and CO_2 concentration in CWD can influence the organisms' activities and decomposition rate, and be restricted to temperature and humidity. With the increase of temperature, biotical

respiration increases, that makes O_2 concentration decrease but CO_2 concentration increase (Paim & Becker 1963). As same as the biotical respiration also increases if humidity reaches to the fiber saturation point (Griffin 1977). But if humidity is high or low excessively, the gas pervasion will be restricted (Tarkow and Stamm 1960).

Woody substrate quality

Diameter

There are different viewpoints on the relationship between CWD size and decomposition rate. Some considers that decomposition is negatively correlated with CWD diameter. Increased CWD diameter results in a smaller surface to volume ratio exposing a minimal portion of exterior CWD to mechanical and biological colonization then decreases decomposition rate (Graham and Cromack 1982; McMinn and Crossley 1993; Marra and Edmonds 1994; Stone *et al*. 1998; Mackensen and Bauhus 2003). Smaller diameter CWD have an increased surface to volume ratio leading to increased fragmentation rates and elevated decomposition rates (Abbott and Crossley 1982; Lambert *et al*. 1980; Foster and Lang 1982). Tool (1965) found that for most of the species studied, small branches had disintegrated after 6 years and only a small portion (<15%) of the large branches and bole had not settled on the ground. But other researches indicated that there is no significant relationship between CWD diameter and decomposition rate especially towards to the big size CWD (Graham and Cromack 1982; Lang 1978; Mattson *et al*. 1987; Edmonds and Eglitis 1989; Marra and Edmonds 1994; Laiho and Prescott 1999). In addition, the high resin content in pine means that pine CWD decay more slowly than those other species such as birch, especially the snags which can last as long as 100 years.

Components

CWD is a complex and heterogeneous substrate with different components (outer bark, inner bark, sapwood and heartwood), which have different proportion and chemical substance/physical character respectively varying with species, size and age, so CWD has different decomposition rate (Harmon 1986). Generally, the inner bark contains the cambium and phloem which are rich in sugars, so inner bark decomposes more rapidly than the other components (Master 1984). Decay may be retarded when the bark sloughs off early, allowing the surface of the sapwood to dry quickly and become casehardened. The heartwood is the most resistant component to decay because it contains some extractives and little nutrient contents (Scheffer and Cowling 1966; Rayner and Boddy 1988). For example, the heartwood of *Thuja plicata* (Scheffer and Cowling 1966), or *Pinus palustris* (Clark 1957) decomposes very slowly even hundreds years. For example, the bark in Monterey pine (*Pinus radia*) logs was determined to have significantly greater lignin concentration and tannin concentration than the other components, possibly explaining the slower decomposition rate of bark (Ganjegunte 2004). Decomposition rate also depends on the chemical composition (lignin, cellulose, hemicelluloses) of components. Lignin decomposes more slowly than celluloses especially in the latter stages of decay, which results in an increase in the lignin/cellulose ratio with the decay process (Crawford 1981).

Species

Different tree species has different decomposition rate; generally, coniferous CWD decomposes more slowly than broadleaved CWD, maybe because coniferous CWD have more simple structure, little live-organize and more lignin contents, but broadleaved CWD has more sugar, amylum and protein, which is easily be decomposed. So the high nutrients content in broadleaved CWD can offer the better conditions for the activities of microbes and other invertebrates. Moreover, sapwood or heartwood components of CWD have different characters with different species. Chen (1992) studied on the decompositions of *Pinus koraiensis* and *Tilia amurensis*, found that decomposition rate had prominent difference between the sapwood and heartwood in *Pinus koraiensis*, but no prominent difference in *Tilia amurensis*.

Organisms

Organisms in the CWD are the most important factor to influence the decomposition rate or type (Harmon 1986), and the influence from all the other controlling factors above mentioned also can be reflected by the variation of organisms. There are many species organisms including the insects, microbes and the soil animals. It is said that there is more life in a dead tree than a living one, largely be made up of fungi and nitrogen-fixing bacteria, both of which are crucial to the health of forest and many studies have confirmed this (Amaranthus 1994; Silvester *et al*. 1982; Aho *et al*. 1974). In dead wood, there is a typical pattern of decay and breakdown, which is largely the result of colonization by organisms. When a tree dies, the sapwood will be invaded by wood-boring beetles (Abbott and Crossley 1982). Along with fungi, bark beetles are among the earlier dead wood colonists, and use the cell contents of the cambium and sapwood. These soon attract predators and parasites including spiders, false scorpions, and ichneumons' wasps, as well as allowing more fungi to enter. Fungi tend to begin the work of decaying the less nutritious heartwood, as their threadlike mycelia penetrate the tissue and allow entry to other organisms. At the final stage of decomposition, insects are replaced by some soil organisms, e.g. Myriapod, Nematoda, Acarina, Collembola and Oligchaeta. Most wood are converted to humus, and that is to say the nutrients that have been stored within the wood for decades return to the soil.

Conclusion

CWD is an integral component of forest ecosystems, acting as a long-term stabilizing storage pool for nutrients (Sollins 1982; Keenan 1993). The ecological function of CWD is only recently being appreciated by foresters and other land managers. So it is essential to develop a comprehensive, long-term and multiplex research system on CWD with colligation of all kinds of subjects.

CWD decomposition is a complex and continuous process and characterizes many biological and physical processes, including biological respiration, leaching and fragmentation. CWD is colonized by decomposer organisms that cause the initial mass loss at the first time (Grier 1978; Fahey 1983; Larho and Prescott 1999). Then the transformation of organic carbon into atmospheric carbon by biological respiration and the polymeric material is changed into soluble substances by the ability of microbes or other organisms. Along with the decomposition, leaching transports the nutrients and soluble polymers into soil matrix, breaks down wood structure and enhances decomposition (McMinn and Crossley 1993). Fragmentation, caused by environmental conditions and biological mechanisms, makes the wood begin to structural deteriorate even elliptical, increases the amount of CWD in contact with the ground and creates a more hospital

condition for invertebrates, bacteria and fungi (Harmon *et al*. 1986). Also biological respiration intensity and leaching can be strengthened and enhanced due to the fragmentation (Edmonds 1980).

During the process of decomposition, biological respiration is critical to quantify the turnover of CWD and its contribution to the C cycle at the regional and global scale. The most important decomposer agents are fungi in terrestrial ecosystems and bacteria in aquatic ecosystems among different microbes, insects, earthworms and collembolans in the colonization (Maser & trappe 1984; Harmon *et al*. 1986). Moreover, site conditions (temperature, humidity, and O_2/CO_2 concentration), woody substrate quality (diameter, species and compound) and the characteristics of organisms in CWD also affected the decomposition harmoniously. For instance, the relationship between size and decomposition may be negative, positive and nonexistent (Foster and Lang 1982; Graham and Cromack 1982; Naesset 1999; Raija and Prescott 2004) largely depending on the site conditions.

Determining the decomposition rate of CWD has been attempted by different mathematical models especially the single-exponential model that relies on changes in volume, biomass and density. It is remarkable that most of studies often measured and reported the loss of density to estimate the decomposition constant assuming that there is no loss of volume (Grier 1978; Lambert *et al*. 1980; Graham and Cranack 1982; Sollins 1982; Fahey 1983; Foster and Lang 1982; Harmon 1986). In fact, due to many complicated processes involved in decomposition such as respiration, leaching and fragmentation, the decomposition constant is the integrated effect of these processes. Respiration and leaching cause the loss of density or weight and the fragmentation cause the loss of volume, especially in the evening of decomposition (Lambert *et al*. 1980; Sollins 1982). So many research results should be lower than the actual one due to without recognizing fragmentation as a decomposition mechanism (Harmon *et al*. 1986; Spies and Franklin 1988; Harmon and Chen, 1991; Marra and Edmonds 1994; Harmon and Sexton 1995).

Nowadays, the increasing attention to CWD function and decomposition makes the management and utilization of CWD in forest become a primary objective on all forest lands and provides an excellent chance to integrate many related research subjects to carry comprehensive, long-term and multi-scale researches which focus on the several sections as follows: (1) The simulation and quantification of the decomposition process and decomposition rate; (2) The modeling erection of biochemistry cycling and nutrients releasing during CWD decomposition; (3) The temporal and spatial characters of CWD decomposition in different forest types; (4) The change of soil physical and chemical properties and microbes community during the CWD decomposition; (5) The long-term response, adaptation and feedback of CWD decomposition on carbon dioxide fluxes and global changes; (6)The effects of natural and anthropogenic disturbance on CWD decomposition and disturbance types; (7)The relationship between CWD decomposition and ecological process integrality and forest health.

References

Abbott, D.T., Crossley, D.A. 1982. Woody litter decomposition following clear-cutting. *Ecology*, **63**(1): 35–42.

Aho, P.E., Seidler, R.J., Evans, H.J., *et al*. 1974. Distribution, enumeration, and identification of nitrogen-fixing bacteria associated with decay in living white fir trees. *Phytopathology*, **64**: 1413–1420.

Amaranthus, M.P., Trappe, J.M., Bednar, L., *et al*. 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. *Can. J. For. Res.*, **24**: 2157–2165.

Arthur, M.A., Fahey, T.J. 1990. Mass and nutrient content of decaying boles in an Engelmann spruce-subalpine fir forest, Rocky Mountain National Park, Colorado. *Can. J. For. Res*., **20**: 730–737.

Ausmus, B.S. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. *Ecol.Bull*, **25**: 180–192.

Barber, B.L., Vanlear, D.H. 1984. Weight loss and nutrient dynamics in decomposing woody loblolly pine logging slash. *Soil Science Society of American Journal*, **48**: 906–910.

Boddy, L. 1983. Carbon dioxide release from decomposing wood: Effect of water content and temperature. *Soil Biology and Biochemistry*, **15**: 501–510.

Boone, R.D., Sollins, P., Cromack, K. 1988. Stand and soil changes along a mountain hemlock death and regrowth sequence. *Ecology*, **69**(3): 714–722.

Brown, S., Mo, J., McPherson, J.K., *et al*. 1996. Decomposition of woody debris in Western Australian forests. *Can. J. For. Res.*, **26**: 954–966.

Bunnell, F.L., Tait, D.E.N., Flanagan, P.W., *et al*. 1977. Microbial respiration and substrate weight loss. II. A model of the influence of chemical composition. *Soil Biology Biochemistry*, **9**: 41–47.

Busse, M.D. 1994. Downed bole-wood decomposition in lodgepole pine forests of central Oregon. *Soil Science Society of America Journal*, **58**(1): 221–227.

Carpenter, S.R. 1981. Decay of heterogeneous detritus: a general model. *Theor. Biol.,* **89**: 539–547.

Chen Hua, Xu Zhenbang. 1991. History, current situation and tendency of CWD ecological research. *Chin. J. Ecol*, **10**(1): 45–50. (in Chinese)

Chen Hua, Xu Zhenbang. 1992. Composition and storage of fallen trees and snags in Korean Pine-deciduous mixed forest at Changbai Mountain. *Chin. J. Ecol*. **11**(1): 17–22. (in Chinese)

Chen, H., Harmon, M.E., Griffiths, R.P. 2001. Decomposition and nitrogen release from decomposing woody roots in coniferous forests of the Pacific Northwest: a chronosequence approach. *Can. J. For. Res.*, **31**: 246–260.

Christensen, O. 1977. Estimation of standing crop and turnover of dead wood in a Danish oak forest. *Oikos*, **28**: 177–186.

Clark, J.W. 1957. Comparative decay resistance of some common pines, hemlock, spruce and true fir. *For. Sci*, **3**: 314–320.

Crawford, R.L. 1981. *Lignin Biodegradation and Transformation*. New York: John Wiley.

Tinker, D.B., Knight, D.H. 2000. Coarse woody debris following fire and logging in Wyoming Lodgepole pine forests. *Ecosystems*, **3**: 472–483.

Dai Limin, Chen Gao, Deng Hongbing, *et al*. 2002. Storage dynamics of fallen trees in a mixed broadleaved and Korean pine forest. *Journal of Forestry Research*, **13**(2): 107–110.

Deng Hongbing, Xiao Baoying, Dai Limin, *et al*. 2002. Advances in ecological studies on in-stream coarse woody debris. *Acta Ecologica Sinica*, **22**(1): 87–93. (in Chinese)

Delaney, M.S., Brown, A.E., Lugo, A., *et al*. 1998. The quantity and turnover of dead wood in permanent forest plots in six life zones of Cenezuela. *Biotropica*, **30**: 2–11.

Deverall, B.J. 1965. The physical environment for fungal growth. 1. Temperature. In: Ainsworth, G.C. & Sussman, A.S. (eds.), *The Fungi. I. The Fungal Cell*. New York: Academic Press, Inc. 543–550.

Edmonds, R.L. 1980. Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock, and Pacific silver-fir ecosystems in western Washington. *Can. J. For. Res.*, **10**: 327–337.

Edmonds, R.L., Eglitis, A. 1989. The role of Douglas fir beetle and wood borers in the decomposition of and nutrient release from Douglas-fir logs. *Can. J. For. Res.*, **19**: 853–859.

Fahey, T.J. 1983. Nutrient dynamic of above ground detritus in lodgepole pine ecosystems, Southeastern Wyoming. *Ecol Monog*, **53**(1): 51–72.

Franklin, J.F., Shugart, H.H., Harmon, M.E. 1987. Tree death as an ecological process. *Bioscience*, **37**: 550–556.

Foster, J.R., Lang, G.E. 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. *Can. J. For. Res*., **12**: 617–626.

Fridman, J., Walheim, M. 2000. Amount, structure and dynamics of dead wood on managed forestland in Sweden. *For. Ecol. Manage.*, **131**: 23–26.

Ganjegunte, G. K., Condron, L. M., Clinton, P. W., *et al*. 2004. Decomposition and nutrient release from radiata pine (*Pinus radiata)* coarse woody debris. *For Ecol Manage*, **187**: 197–211.

Gardiner, L.M. 1957. Deterioration of fire-killed pine in Ontario and the causal wood-boring beetles. *Can. Entomol*, **89**: 241–263.

Girisha, K., Condron, L.M., Clinton, P.W., *et al*. 2004. Decomposition and nutrient release from radiate pine (*Pinus radiate*) coarse woody debris. *For. Ecol. Manage.*, **187**(2-3): 197–211.

Golladay, S.W., Webster, J.R. 1988. Effects of clear-cut logging on wood breakdown in Appalachian Mountain streams. *The American Midland Naturalist*, **119**: 143–155.

Graham, R.L., Cranack, K.J. 1982. Mass, nutrient and decay rate of dead boles in rain forests of Olympic National Park. *Can. J. For. Res.*, **12**: 511–52.

Graham, S.A. 1925. The felled tree trunk as an ecological unit. *Ecology*, **6**: 397–416.

Graham, R.L., Cromack, K. 1982. Mass, nutrient content and decay rate of dead boles in rain forests of Olympic National Park. *Can. J. For. Res.*, **12**: 511–521.

Gray, A.N., Spies, T.A. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. *Ecology*, **78**: 2458–2473.

Grier, C.C. 1978. A *Tsuga heterophylla–Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. *Can. J. For. Res.*, **8**: 198–206.

Griffin, D.M. 1977. Water potential and wood decay fungi. *Ann. Rev. Phytopathol.*, **15**: 319–329.

Harmon, M.E., Cromack, K., Smith, B.G. 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. *Can. J. For. Res.*, **17**: 1256–1272.

Harmon, M.E., Ferrel, W.K., Franklin, J.F. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science*, **247**: 699–702.

Harmon, M.E., Franklin, J.F., Swanson, F.J., *et al*. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, **15**: 133–302.

Harmon, M.E., Franklin, J.F. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology*, **70**(1): 48–59.

Harmon, M.E., Chen, H. 1991. Coarse woody debris dynamics in two old growth ecosystems. *Bioscience*, **41**: 604–610.

Harmon, M.E., Sexton, J. 1995. Water balance of conifer logs in early stages of decomposition. *Plant and Soil*, **172**: 1141–1521.

Harmon, M.E., Krankina, O.N., Sexton, J. 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. *Can. J. For. Res.*, **30**(1): 76–84.

Hou Ping, Pan Cunde. 2001. Coarse woody debris and its function in forest ecosystem. *Chin. J. Appl. Ecol.*, **12**(2): 309–314. (in Chinese)

Holub, S.M., Lajtha, K., Spears, J.D. 2001. A reanalysis of nutrient dynamics in coniferous coarse woody debris. *Can. J. For. Res.*, **31**: 1894–1902.

Janisch, J.E., Harmon, M.E. 2001. Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. *Tree Phys.*, **22**: 77–89.

Jemison, G.M. 1937. Loss of weight of wood due to weathering. *J. For.*, **35**: 460–462.

Käärik, A.A. 1974. Decomposition of wood. In*:* Biology of plant litter decomposition. Dickson, C.H. & Pugh, G.J.E. (eds.), **1**: 129–174. London: Academic Press.

Laiho, R., Prescott, C.E. 1999. The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. *Can. J. For. Res.*, **29**: 1502–1603.

Lambert, R.C., Lang, G.E., Reiners, W.A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology*, **61**(6): 1460–1473

Lang, G.E., Forman, R.T.T. 1978. Detritus dynamics in a mature oak forest: Hutchenson Memorial Forest, New Jersey. *Ecology*, **59**(3): 580–595.

Leach, J.G., Orr, L.W., Christensen, C. 1934. The interrelationships of bark beetles and blue-staining fungi in felled Norway pine timber. *J. Agric. Res.*, **49**: 315–341.

Li Ke, Li Fengzhen. 1992a. Variation of biochemical and ecological properties of fallen trees during decomposition process. Research of forest ecosystem, **6**: 222–226. (in Chinese)

Li Ke, Li Fengzhen. 1992b. Research on fallen tree decomposition fungi in Changbai Mountain. *Research of Forest Ecosystem*, **6**: 210–214. (in Chinese)

Li Linghao, Dang Gaodi, Wang Tiejun, *et al*. 1998. Coarse woody debris in an abies fargesh forest in the Qinling Mountains. *Acta Phytoecologica Sinica*, **22**(15): 434–440. (in Chinese)

Li Linghao, Xing Xuerong, Huang Daming, *et al*. 1996. Storage and dynamics of coarse woody debris in *Castanopsis eyrei* forest of Wuyi Mountain, with some considerations for its ecological effects. *Acta Phytoecologica Sinica*, **20**(2): 132–143. (in Chinese)

Liu Huiying, Zhang Siyu, Ji Xia. 2004. The soil and water conservation functions of coarse woody debris. *World Forestry Research*, **17**(3): 25–28. (in Chinese)

Liu Wenyao, Xie Shouchang, Xie Kejin, *et al*. 1995. PreIiminary studies on the litter fall and coarse woody debris in Mid-mountain humid evergreen broad-leaved forest in Ailao Mountains. *Acta Botanica Sinica*, **37**(10): 807–814. (in Chinese)

Marra, J.L., Edmonds, R.L. 1994. Coarse woody debris and forest floor respiration in an old-growth coniferous forest on the Olympic Peninsula, Washington, USA. *Can. J. For. Res.*, **24**: 1811–1817.

Maser, C., Trappe, J. M. 1984. *The seen and unseen world of the fallen tree* (Tech. Eds.). Portland, Oregen: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Mackensen, J., Bauhus, J. 2003. Density loss and respiration rates in coarse woody debris of *Pinus radiata, Eucalyptus regnans* and *Eucalyptus maculata*. *Soil Biology and Biochemistry*, **35**: 177–186.

Mattson, K.G., Swank, W.T. 1984. Carbon dioxide fluxes from conventional and whole tree harvested watersheds-effects of wood residue. *Bulletin of the Ecological Society of America*, **65**: 123.

Mattson, KG., Swank, W.T., Waide, J.B. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the southern Appalachians. *Can. J. For. Res.*, **17**: 712–721.

McMinn, J.W., Crossley, D.A. 1993. Biodiversity and coarse woody debris in southern forests. *USDA Forest Service. Report*: SE–94.

Mikola, P. 1960. Comparative experiments in decomposition rates of forest litter in southern and northern Finland. *Oikos*, **11**: 161–166.

Minderman, G. 1968. Addition, decomposition and accumulation of organic matter in forests. *J. Ecol.*, **56**: 355–362.

Naesset, E. 1999. Decomposition rate constants of *Picea abies* logs in southeastern Norway. *Can. J. For. Res.*, **29**: 372–381.

Niklas, D., Karin, J., Christer, N. 2005. Long-term dynamics of large woody debris in a managed boreal forest stream. *For. Ecol. Manage*, **210**: 363–373.

Olson, J.S. 1963. Energy storage and the balance of producers and decomposition in ecological systems. *Ecology*, **44**: 332–341.

Paim, U., Becker, W.E. 1963. Seasonal oxygen and carbon dioxide content of

decaying wood as a component of *Orthosoma brunneum*. *Can. J. For. Res.*, **41**: 1133–1147.

Rabe, M.J., Morrell, T.E., Green, H., *et al*. 1998. Characteristics of ponderosa pine snag roosts used by reproductive bats in northern Arizona. *J. Wildl. Manage*, **62**(2): 612–621.

Raija, L., Prescott, C.E. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. *Can. J. For. Res.*, **34**: 763–777.

Rayner, A.D., Boddy, L. 1988. Fungal communities in the decay of wood. *Adv. Microb. Ecol.*, **10**: 115–166.

Savely, H.E. 1939. Ecological relations of certain animals in dead pine and oak logs. *Ecological Monographs*, **9**: 322–385.

Scheffer, T.C., Cowling, E.B. 1966. Natural resistance of wood to deterioration. *Annual Review of Phytopathology*, **4**: 147–170.

Silvester, W.B., Sollins, P., Verhoeven, T., *et al*. 1982. Nitrogen fixation and acetylene reduction in decaying conifer boles: effects of incubation time, aeration, and moisture content. *Can. J. For. Res.*, **12**: 646–652.

Singh, J.S., Gutpka, S.R. 1977. Plant decomposition and soil respiration in terrestrial ecosystem. *Bot. Rev.*, **43**: 449–528.

Sollins P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res.*, **12**: 18–28.

Spies, T.A., Franklin, J.P., Thomas, T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology*, **69**: 1689–1702.

Stone, J.N., MacKinnon, A., Parminter, J.V., *et al*. 1998. Coarse woody debris decomposition documented over 65 years on southern Vancouver Island. *Can. J. For. Res.*, **28**: 788–793.

Swift, M.J. 1973. The estimation of mycelial biomass by determination of the hexoamine content of wood tissue decayed by fungi. *Soil Biology & Biochemistry*, **5**: 321–332.

Swift, M.J. 1977. The ecology of wood decomposition. *Science Progress*, **64**: 175–199.

Swift, M.J., Heal, O.W., Anderson, J. 1979. *Decomposition in terrestrial ecosystems*. Berkeley: University of California Press.

Tang Xuli, Zhou Guoyi, Zhouxia, *et al*. 2003. Coarse woody debris in monsoon evergreen broad-leaved forests of Dinghushan Nature Reserve. *Acta Phytoecologica Sinica*, **27**(4): 484–489. (in Chinese)

Tarkow, H., Stamm, A.J. 1960. Diffusion through air-filled capillaries of softwoods. Part I. Carbon dioxide. *For. Prod. J.*, **10**: 247–250.

Timothy, S.M., Mark, J.K.2004.Demographic responses of shrews to removal of coarse woody debris in a managed pine forest. *For. Ecol. Manage.*, **189**: 387–395.

Tools, E.R. 1965. Deterioration of hardwood logging slash in the South. Tech. Bull. No.1328. Washington, D.C.: U.S. Department of Agriculture Forest Service

Torgersen, T., Bull, E. 1995. Down logs as habitat for forest-dwelling ants-the primary prey of pileated woodpeckers in northeastern Oregon. *Northwest Science*, **69**: 294–303.

Turner, D.P., Koerper, G.J., Harmon, M.E., *et al.* 1995. A carbon budget for forests of the conterminous United States. *Ecol. Appl.*, **5**: 421–436.

Tyrrel, L.E, Crow, T.R. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. *Ecology*, **75**: 370–386.

Wei, X.H., Kimmins, J.P., Peel, K., *et al*. 1997. Mass and nutrients in woody debris in harvested and wildfire-killed lodge pole pine forests in the central interior of British Columbia. *Can. J. For. Res.*, **27**: 148–155.

Wieder, R.K., Lang, G.E. 1982. Acritique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology*, **63**: 1636–1642.

Woldendrop, G., Keenan, R.J., Barry, S., *et al*. 2004. Analysis of sampling methods for coarse woody debris. *For. Ecol. Manage*, **198**: 133–148.

Wu Jiabing, Guan Dexin, Han Shijie, *et al.* 2005. Ecological functions of coarse woody debris in forest ecosystem. *Journal of Forestry Research*, **16**(3): 247–252.

Xu Huacheng. 1998. *China Daxinganling forest*. Beijing: Science Press. (in Chinese)

Yan Enrong, Wang Xihua, Huang Jianjun. 2005. Concept and classification of coarse woody debris in forest ecosystems. *Acta Ecologica Sinica*, **25**(1): 158–167. (in Chinese)

Yang Liyun, Dai Limin, Zhang Yangjian. 2002a. Storage and decomposition of fallen wood in dark coniferous forest on the North Slope of Changbai Mountain. *Chin. J. Appl. Ecol.*, **13**(9): 1069–1071. (in Chinese)

Yang Liyun, Dai Limin. 2002b. The decomposition and nutrient content of fallen woods in the moss-*Pinus koraiensis* dark-conifer forest at North Slope of Changbai Mountain. *Acta Ecologica Sinica*, **22**(2): 185–189. (in Chinese)

Yoneda, T. 1975. Studies on the rate of decay of wood litter on the forest floor. Part 2: Dry weight loss and carbon dioxide evolution of decaying wood. *Japanese Journal of Ecology*, **25**: 132–140.

Zhao Xiuhai. 1995. Effect of fallen tree on natural regeneration in Korean Pine-deciduous mixed Forest of Changbai Mountain. *Journal of Jilin Forestry University*, **11**(4): 200–204. (in Chinese)

Zhao Yutao, Yu Xinxiao, Cheng Genwei, *et al*. 2002. A slighting tache in field of forest hydrology research-hydrological effects of coarse woody debris. *Journal of Mountain Science*, **20**(1):12–18. (in Chinese)

Zhong, H., Schowalter, T.D. 1989. Conifer bole utilization by wood-boring beetles in western Ontario. *Can. J. For. Res.*, **19**: 943–947.

Zimmerman, J.K., Pulliam, W.M., Lodge, D.J., *et al*. 1995. Nitrogen immobilization by decomposing woody debris and the recover of tropical wet forest from hurricane damage. *Oikos*, **72**: 314–322.